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Interference effect of observed human movement on action is due to velocity profile of biological motion

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It has previously been shown that observing an action made by a human, but not by a robot, interferes with executed actions (Kilner, Paulignan, & Blakemore, 2003). Here, we investigated what aspect of human movement causes this interference effect. Subjects made arm movements while observing a video of either a human making an arm movement or a ball moving across the screen. Both human and ball videos contained either biological (minimum jerk) or non-biological (constant velocity) movements. The executed and observed arm movements were either congruent (same direction) or incongruent (tangential direction) with each other. The results showed that observed movements are processed differently according to whether they are made by a human or a ball. For the ball videos, both biological and non-biological incongruent movements interfered with executed arm movements. In contrast, for the human videos, the velocity profile of the movement was the critical factor: only incongruent, biological human movements interfered with executed arm movements. We propose that the interference effect could be due either to the information the brain has about different types of movement stimuli or to the impact of prior experience with different types of form and motion.

INTRODUCTION

The idea that actions are intrinsically linked to perception (James, 1890) has become increasingly accepted recently (Jeannerod, 1994; Prinz, 1997). This is in part due to the discovery of mirror neurons in monkey ventral premotor cortex. These neurons discharge both when the monkey executes specific hand movements and when it observes another monkey or human executing the same movements (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Fogassi, & Gallese, 1996a; Rizzolatti, Fogassi, & Gallese, 2001). There is a large body of evidence that in humans several brain regions are activated both during action generation and during observation of others' actions (Decety et al., 1997; Hari et al., 1998; Rizzolatti et al., 1996b). In some brain regions the overlap between action observation and action execution is highly specific. Action observation activates premotor cortex in a somatotopic manner—watching mouth, hand,

and foot movements activates the same functionally specific regions of premotor cortex as making those respective movements (Buccino et al., 2001).

Observing a movement also has measurable consequences on the peripheral motor system. During action observation there is a significant increase in the motor-evoked potentials from the hand muscles that would be used if making such a movement (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995). In addition, reaction times to initiate a finger movement are significantly slowed down after the visual presentation of photographs of different finger movements (Brass, Bekkering, & Prinz, 2001). This suggests that, during observation of action, the specific neural networks subserving that particular movement are already tuned for action (Jeannerod, 1994; Prinz, 1997).

Indeed, it has been shown that observing someone else make a movement has a measurable interference effect on qualitatively different simultaneously executed movements (Kilner, Paulignan, & Blakemore, 2003). In this experiment, subjects made sinusoidal movements with their right arm at the same time as observing movements that were either congruent (same direction) or incongruent (tangential direction) with their own movements. Variance in arm movement was used as an index of interference to the executed arm movement. Compared with the baseline condition in which subjects made arm movements without watching anything, there was significantly increased variance in subjects' arm movements when they observed another human making arm movements that were incongruent with their own. In contrast, variance was not increased when the observed incongruent movement was made by a robotic arm. Thus, the interference effect was not simply due to increased attentional demands or task complexity or any other artifactual effect of observing an incongruent movement. These results suggest that observed movements are processed differently according to whether they are made by a human or a robot.

However, it is not known what aspect of human movement, which is not present in robotic movement, causes the interference effect. There are several differences between humans and robots. First, human movements typically have a particular non-linear velocity profile. Point to point movements of the human arm tend to follow a minimum jerk (MJ) trajectory (Hogan,

1984), in which the movement starts slowly, accelerates smoothly to a peak velocity near the midpoint and then decelerates slowly. This results in a smooth, bell-shaped velocity profile (Abend, Bizzi, & Morasso, 1982), where mathematically the derivative of acceleration (jerk) is minimized over the movement. The bell-shaped velocity profile of human movements contrasts with the constant velocity profile of physical objects (such as the robot used in the above experiment) governed by Newton's laws. Second, humans do not move in perfectly straight lines, rather the trajectory of the hand is constrained by the dynamics of the arm and deviates in a systematic fashion from a linear path (Abend et al., 1982). Third, humans have features such as a face and limbs. The robot used in the Kilner et al. (2003) experiment was non-humanoid, and had no face-like structure, although in a very general sense it shared some resemblance to a human form since it comprised a main "trunk" with an attached "arm" that could move in three dimensions.

The aim of the current study was to investigate whether the interference effect of observed human action on executed action was specific to the observation of a biological motion trajectory, to the observation of a human form, or to some combination of these factors. The interference effect found in Kilner et al. (2003) is likely to be mediated by the human mirror neuron system (MNS), but the question of whether the human MNS responds to the behavior of non-human actors is currently controversial. Some studies (Tai, Scherfler, Brooks, Sawamoto, & Castiello, 2004) suggest that responses in premotor cortex to observed motion is specific to human action and this area does not respond to robotic movements. Other data suggest equivalent neural responses to both observed human action with a natural MJ trajectory and robotic action with a CV trajectory (Gazzola, Rizzolatti, Wicker, & Keysers, 2007). In the current study, we used a behavioral measure of motor interference to assess the impact of different types of observed action on the MNS.

Specifically, we investigated whether it was the form or movement type that caused the interference effect found in our previous study (Kilner et al., 2003). To distinguish between movement velocity profile and features of the moving effector, we created video stimuli and manipulated two aspects of the movement: (1) effector

type, whether the stimulus was human or a ball; and (2) movement type, whether the stimulus moved with minimum jerk (MJ) or constant velocity (CV) profile. The velocity profile of the observed movement was manipulated by using a high-speed video camera to film a human arm movement and then digitally altering the video, frame-by-frame, to create a video of an arm movement with constant velocity. Therefore, there were two types of human movement video: keeping all other factors constant, one video type showed normal, biological (MJ) arm movement and the other showed the same human arm moving with non-biological (CV) motion. In addition, in another set of videos, we replaced the human with a ball, producing two further videos: a ball moving with biological motion (MJ), and a ball moving with CV. Subjects made arm movements while observing the above videos of a human or a ball moving either in the same direction (congruent) or tangential (incongruent) to the subject's own movements.

Based on our previous study, it was predicted that interference would occur to an executed movement when subjects observed another human making incongruent MJ movements. Since human CV movement is similar to the robot's movement in our previous study (Kilner et al., 2003), we did not expect to see interference in the condition in which subjects observed a human making incongruent CV movements. Predictions for the ball condition were more complex. If the interference effect is driven solely by the perception of incongruent MJ movements (regardless of form), we would also expect interference from the MJ ball but not from the CV ball. In contrast, if the interference effect is specific to the observation of a human form with MJ movement, we would not expect to see any interference from the ball. Finally, if the interference effect is modulated by the type of information present in the ball stimulus, or by prior experience of how balls tend to move in the world, interference could be found in both incongruent ball conditions. The results of this study will shed light on these possibilities.

METHODS

Subjects

Fifteen healthy, right-handed undergraduates and postgraduates from UCL took part in the study.

Informed consent was obtained from each subject and the study was approved by the local ethics committee.

Experimental design

We generated video stimuli of humans and objects (a ball) with constant velocity (CV) and biological (MJ) motion by filming an actor performing several horizontal and vertical forearm movements with a high-speed digital video camera (Photron Europe, Buckinghamshire, UK, www.photron.com) at 250 frames and a resolution of 512×480 pixels. A single characteristic movement example of a horizontal movement and a vertical movement, each lasting 800 ms (200 frames) was selected and the location of the fingertip in each frame was recorded. To generate stimuli depicting the actor moving with a CV profile, 20 frames were selected from each set of 200, such that the fingertip maintained a CV over the frames. These 20 frames were repeated in reverse order to generate a 40 frame video clip of a complete horizontal or vertical movement cycle. To create stimuli depicting the actor moving with a MJ velocity profile, every tenth frame from the original high-speed movies was selected and assembled first forward and then in reverse order, maintaining the natural velocity profile of the actor's movement over the 40-frame clip.

Ball stimuli were created by generating a set of images with a blue background and a white disc at the location of the fingertip in each human movie. Thus each ball clip contained identical dynamic information to that in each human clip; the only difference between the human and ball videos was the form of the moving object. In all the clips, a complete cycle of movement took 1.6 seconds (40 frames).

There were nine video conditions, eight of which formed a $2 \times 2 \times 2$ factorial design (see Figure 1). The factors were: (1) Observed movement velocity (MJ or CV); (2) Observed effector (dot or human); and (3) Congruency between observed and executed movement (same or tangential direction). In addition to these video conditions, there was a baseline condition in which a fixation cross on a blue screen was presented to the subject.

The videos were rear-projected onto a flat screen (width 100 cm $\times$ height 80 cm) positioned 50 cm in front of the subject who was sitting on a chair. While watching the videos each subject was
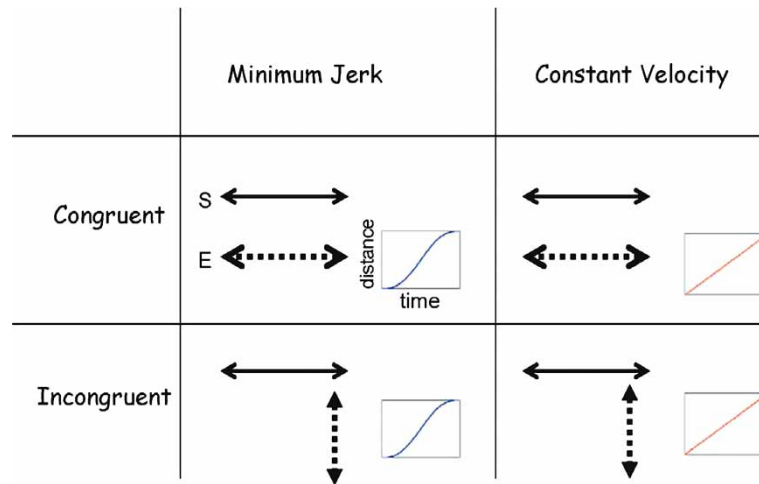
Figure 1. Experimental design. Subjects (S in left upper cell), who were seated, made sinusoidal movements with their right forearm at the same time as watching videos of movements of an effector (E in left upper cell). The observed effector was either a human or a ball. Observed movements were either minimum jerk (with a curved velocity profile as shown in the graphs in the left-hand column) or constant velocity (with a linear velocity profile as shown in the graphs in the right-hand column). Observed movements were either in the same direction (congruent) or tangential direction (incongruent) from the subject's executed movements. In addition, there were two baseline conditions in which the subject moved their forearm either horizontally or vertically while watching a fixation cross in the centre of the screen.

instructed to make movements (either horizontal or vertical) of their right forearm at a rate of 1.6 Hz. The subject was instructed to watch the index finger of the human, or the ball, or the fixation cross, in the videos. No other instruction was given. Before the experiment, subjects practised the movement until they were proficient at producing the desired forearm movements at the correct pace and amplitude. This took under one minute for each subject.

Each participant completed 5 trials for each of the nine conditions above while moving his or her arm in a horizontal direction, and 5 trials for each condition while moving his or her arm vertically. Trial order was fully randomized. Each trial began with a written instruction (''Move horizontally starting from the left'' or ''Move vertically starting from the top'') on a black screen. The screen color then changed to blue and the computer gave a sequence of alternating low and high beeps at 800 ms intervals for three cycles. The participant was instructed to move his or her arm in time with the beeps, to reach the right, or bottom, position on the low beep and the left, or top, position on the high beeps. This ensured that when the video clip started after three cycles, the participant's movement was already synchronous with the visual image. After the sixth beep, the screen immediately displayed the video clip of a human or ball moving at 1.6 Hz, and the clip was repeated 10 times. Thus,

participants performed 13 complete movement cycles on each trial, three cycles with beeps and no video and 10 with the video stimulus and no beeps. Breaks were provided between trials to prevent fatigue.

Data acquisition

The position of the participant's hand during every trial was recorded using a Flock of Birds (http://www.ascension-tech.com/products/flockofbirds.php) magnetic motion tracking system, which returns the position and orientation of markers in space at 100 Hz. A single marker was attached to the participant's fingertip, and the magnetic tracking unit was placed below the video screen. A customized C program was used to play the sounds and videos and to record the marker position in 3D space.

Data analysis

Data were low-pass filtered at 10 Hz using a 2nd order Butterworth filter. We analyzed only the final 12.8 seconds (8 cycles) of each trial for two reasons. First, we omitted the first two cycles to avoid the data being affected by the ''surprise'' of the visual stimulus appearing on the screen. Second, this allowed time for the subject's arm

movement to align with the visual stimulus. Although subjects were not instructed to align their movement with the visual stimulus, they naturally did this and it took up to 2 cycles to achieve. Data were segmented offline into movements from right to left and those from left to right for horizontal conditions and for those from up to down and from down to up for the vertical movements (Figure 2). Therefore there was a maximum of 40 segmented movements per condition per subject. For each segmented movement the variance in the movement orthogonal to the dominant dimension of movement, and in the dominant dimension of the incongruent movement, was calculated. Thus if the subject made a movement from left to right, the X dimension was the dominant movement dimension and the variance was calculated for the movements in the Z dimension, and vice versa. The mean of these variances was calculated across all trials for each condition. The mean variance for each participant in each trial was analyzed using repeated measures ANOVAs and paired t-tests as described below.

RESULTS

An initial repeated measures $2 \times 2 \times 2 \times 2$ ANOVA was carried out on the factors performed Movement Direction (horizontal vs. vertical), Movement Congruency (congruent vs. incongruent), Observed Actor (human or ball) and Movement Type (MJ or CV). The results of this ANOVA revealed a significant main effect of movement direction, $F(1, 14) = 17.509$, $p = .001$, with a significantly greater variance for vertical than horizontal movements. There was also a significant main effect of movement congruency, $F(1, 14) = 12.827$, $p = .003$, with greater variance when observing incongruent movements than congruent movements. There was a significant interaction between movement direction and movement congruency, $F(1, 14) = 5.958$, $p = .029$ (see Figure 2A). There was a significant main effect of observed effector, $F(1, 14) = 9.205$, $p = .009$, and a significant interaction between movement direction and observed effector, $F(1, 14) = 6.266$, $p = .025$ (see Figure 2B). In addition, there was a significant interaction between observed effector and movement type, $F(1, 14) = 5.919$, $p = .029$ (see Figure 2C). No other main effects or interactions were significant.

As there was a significant interaction between the movement direction and movement congruency, subsequent analyses were performed to investigate effects for horizontal and vertical movements separately. Furthermore, because there was a significant interaction between observed actor and movement type, human and ball conditions were analyzed separately. Therefore, all subsequent analyses consisted of 2×2 ANOVAs where the factors were movement congruency and movement type for horizontal and vertical movements, and for observing a human or a ball. There were no significant main effects or interactions ($p > .05$) when the subjects were making horizontal movements. Therefore, the following analyses are for vertical executed movements only.

When subjects made vertical movements and observed a *human* there was a trend towards a main effect of congruency although this did not reach significance, $F(1, 14) = 3.945$, $p = .067$.
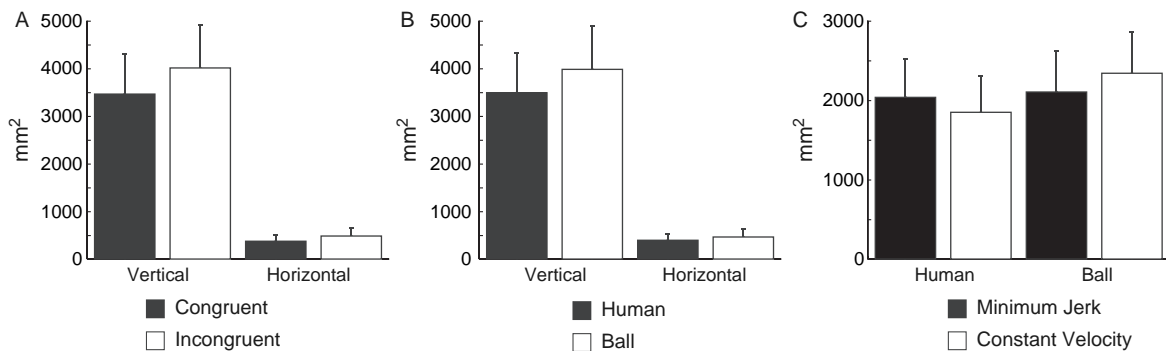

Figure 2. Interactions. The three panels show the mean variances in square millimeters tangential to the axis of movement. Panel A illustrates the interactions between movement direction and movement congruency. Panel B illustrates the interaction between movement direction and observed effect. Panel C illustrates the significant interaction between observed effector and movement type. In all panels the error bars represent the standard error.

There was a significant interaction between movement congruency and movement type, $F(1, 14) = 7.366$, $p = .017$ (see Figure 3). This interaction was driven by an increase in variance when observing an incongruent MJ relative to a congruent MJ human movement, $t(14) = 3.2551$, $p < .05$. Variance in the incongruent MJ condition was also significantly greater than variance in the baseline condition, $t(14) = 2.2960$, $p < .05$, paired t-test, two tailed.

When subjects made vertical movement observing a *ball* there was only a main effect of congruency, $F(1, 14) = 4.746$, $p = .047$. There was no significant interaction between congruency and movement type, $F(1, 14) = 0.203$, $p = .659$. There was significantly greater variance for both MJ and CV incongruent conditions compared with baseline (see Figure 3); $t(14) = 2.9601$, $p < .05$; $t(14) = 3.6152$, $p < .05$, respectively.
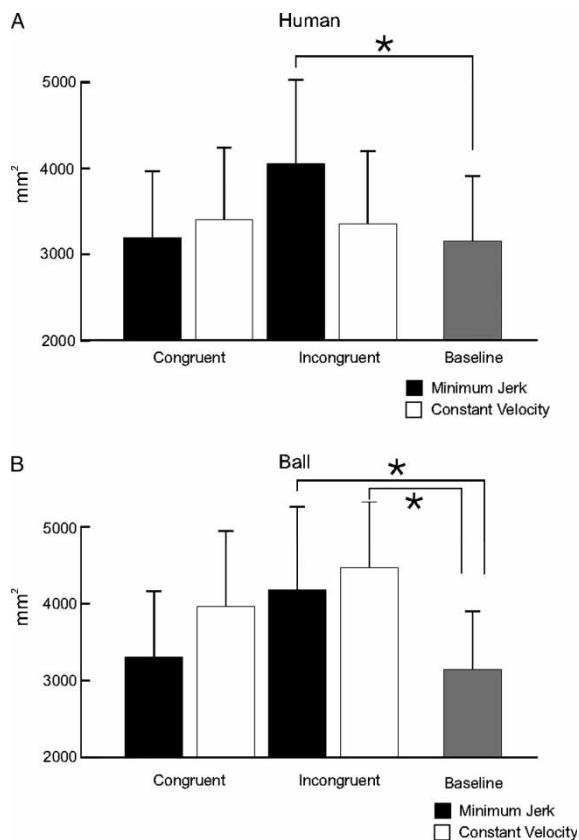

Figure 3. Vertical movements. The two panels show the mean variances in square millimeters tangential to the axis of movement for the vertical movements only. Panel A shows the mean variance for each of the conditions while observing a human. Panel B shows the mean variance for each of the conditions while observing a ball. The gray bar in both panels shows the mean variance during the baseline condition. In both panels the error bars represent the standard error.

DISCUSSION

The present results demonstrate that observing incongruent moving stimuli presented on a video display (rather than live) can have a measurable interference effect on simultaneously executed actions. The precise nature of this effect depends on type of movement present in the video stimuli, with interference found for observation of a human making biological (minimum jerk) movements but not for a human making non-biological (constant velocity) movements. In contrast, when the stimulus was more abstract (a moving ball), interference was found for both velocity profiles.

The results replicate our previous study demonstrating that observing arm movements made by a human has a significant interference effect on ongoing executed movements when the observed and executed movements are incongruent. As we found in our previous study, there was no significant interference to executed movements when the observed human movement was congruent with executed movements. However, these new data extend our previous study by showing that the interference effect is only present when the incongruent observed human movements are biological (MJ; Figure 3A). There was no significant interference to ongoing executed movements if the observed incongruent human movements were non-biological (CV). This condition is similar to the condition in our previous study in which subjects observed a robot (with a non-MJ velocity profile) making incongruent movements. In this condition there was no interference effect on executed movement. The finding that observing a human making incongruent CV movements had no significant effect on executed movement demonstrates that the interference effect found for human incongruent MJ movements is not simply due to increased attentional demands, task complexity or any other artifactual effect of observing an incongruent movement. Rather, it suggests that the brain processes MJ and CV movements differently when they are made by a human. Taken in isolation these results suggest that the interference effect when observing a human making incongruent movement is due to the biological nature of human movement, rather than to the form of the human body.

The question then remains, what happens when we change the form of the observed movement? Based on the results when observing a

human we predicted that, for the ball, there would either be the same interference effect, i.e., the interference effect is form-invariant, or no interference effect, i.e., the presence of a human form is essential to illicit an interference effect. Neither of these predictions was realized. Instead, observing a ball interfered with executed movements if the observed ball movements were incongruent with executed movement direction, irrespective of whether the observed ball movements were biological or not. Thus, the finding that only MJ movements interfere with executed movement seems to be specific to observed human movement.

The reason for the difference in the interference effect between observing a ball and observing a human requires further investigation. Here we suggest two alternative explanations, based on knowledge of the different parts of the MNS that could mediate the interference effect. The first explanation focuses on the perception of biological motion stimuli in the superior temporal sulcus (STS), which is connected to both the premotor and inferior parietal regions of the MNS (Catani, Jones, & Ffytche, 2005). The second explanation focuses on the overlap of perceptual and motor processing of human actions in the parietal and premotor parts of the MNS (Gallese et al., 1996; Rizzolatti et al., 1996a, 2001).

There is extensive evidence that parts of the visual system discriminate between different types of motion stimuli, in particular between biological and non-biological motion. Three-month-old babies can discriminate between displays of moving dots that have biological motion and displays in which the same dots move randomly (Bertenthal, 1993). This ability has been associated with the STS, which responds selectively to biological motion in monkeys (Oram & Perrett, 1994) and in humans (Allison, Puce, & McCarthy, 2000; Frith & Frith, 1999). The STS may provide visual input to the MNS (Catani et al., 2005), so any modulation in neuronal activity in the STS could have a direct effect on the engagement of the MNS during action observation. The ventral bank of the posterior STS is activated by displays of moving dots showing a walking person (biological motion) compared with displays in which the same dots move at equal velocity in the same direction (Grossman et al., 2000) or have rigid object motion (Grèzes et al., 2001).

These data suggest that the detection of biological motion is hardwired in the human

brain at an early age, which would lead to an automatic classification of observed motion as biological or non-biological. Our results for human videos and from our previous study (Kilner et al., 2003) are in line with the proposal that observed movements are classified as biological (MJ) or non-biological (CV) and treated differently accordingly. The next question is why such a distinction is only present for human movements, and not for ball movements, in the current study. One possibility is that there is not sufficient information in the ball stimulus for the biological and non-biological movements to activate differentially neurons in the STS. The ball stimuli in the current study are very different from those used in point-light displays. Point-light displays generally depict movements of whole bodies comprised of several points of light. Information about the nature of the movement can be extracted from the relative movements of the points of light. In contrast, the ball stimuli in the current study show just one dot moving across a screen and therefore there is no information about relative movements. Such a hypothesis predicts that there would not be differential STS activity when observing the ball with MJ or CV. In this case the CV ball would be processed in the same way as the MJ ball, which would explain why a similar interference effect was observed to both incongruent ball stimuli. Note that the relative spatial information is present when observing the human, which would result in a differential interference effect to incongruent CV and MJ human movements.

The second possible explanation is based on the proposal that the interference effect is mediated by the premotor or parietal regions of the MNS. The human MNS responds to both executed and observed actions (Rizzolatti et al., 2001), and therefore might mediate the interference between executed and observed actions found in the present study. Recent studies suggest that the response of the human MNS to observed actions is strongly modulated by prior experience of the actions (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005; Cross, Hamilton, & Grafton, 2006). In everyday life, we have extensive experience of seeing humans move with a MJ trajectory, but we never see humans move with a CV trajectory. Thus, the MNS is likely to respond, and interference be obtained, for human MJ but not for human CV stimuli. Humanoid figures that move with a MJ trajectory are likely to be familiar enough to

be simulated and would cause interference, as found by Oztop, Franklin, Chaminade, and Cheng (2005). In contrast, the MNS is not likely to respond to observation of an industrial robot moving with an unfamiliar CV trajectory, as in Kilner et al. (2003), and interference was not seen in this condition.

This MNS explanation may also be able to account for the ball results of the current study. The premotor regions that form part of the human MNS and which respond to observed actions can also respond to the observation of sequenced, non-biological stimuli (Schubotz & von Cramon, 2004). Most people are familiar with balls or similar computer graphics moving with a wide variety of trajectories, including MJ and CV. It is possible that premotor regions are able to simulate, or predict, the movements of these familiar stimuli, and that this results in an interference effect for a ball regardless of the precise trajectory of the ball. In contrast, the MNS may not able to simulate the behavior of stimuli that are novel, for example some robots, and therefore such stimuli would not cause interference even when presented incongruent to the participant's own movement. A prediction of this theory is that participants with an unusual experience profile, for example, people who work with industrial robots, might also show interference effects from robots.

In the current study there were only significant effects when subjects made vertical, as opposed to horizontal, movements. In addition, the variance overall was significantly greater for vertical than horizontal effects. This is in contrast to the results of our previous study when horizontal movements were associated with more variance than vertical movements. These differences can be explained by a difference in the experimental design between the two studies. In our previous study, subjects were standing and movement in the vertical plane were made to the side of the body. In the current study subjects were seated. It is possible that, first, this stabilizes the movement in the horizontal direction resulting in lower sensitivity to the incongruency effects. Second, being seated might have prohibited a free vertical movement. Subjects typically made "J" shaped movements in all trials resulting in an increase in variance in the orthogonal dimension to that in which the intended movement should have been made. However, it should be noted that this can not explain the task-specific modulations in variance for the vertical movements. Thus, the interference effect can be seen in arm movements if subjects are seated or standing, but the direction differences should be borne in mind when designing future experiments.

Summary

In this study, we found that observed human movements interfere with incongruent executed arm movements only when they are biological (MJ). Observed non-biological (CV), incongruent human movements had no interference effect on executed movements. In contrast, observed ball movements interfere with incongruent executed arm movements whether they are MJ or CV. This effect could be due to the quantity of information the brain has to distinguish different types of motion stimuli, or the impact of prior experience with different types of form and motion. Further research is needed to discriminate between these possibilities.

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